FERTILISATION OF PAPILIONACEOUS FLOWERS—CORONILLA

IN NATURE, vol. vi. pp. 478 and 498, you inserted a paper of mine in which an attempt was made to draw certain general conclusions concerning the fertilisation of papilionaceous flowers from the examination of a few genera, chiefly English: and in that paper I stated that the foreign genus *Coronilla* presented peculiar difficulties. I have since then been stimulated by Mr. Darwin's kind interest to examine *Coronilla* more carefully, and now send you the results.

The ultimate result of these generalisations was that in all the following particulars, viz. the position and motion of the flowers and the peduncle, the cohesion of the petals, the cohesion of the stamens (so remarkable a feature in this tribe); the structure and character of the filaments, of the anthers, and of the pollen, the structure of the style and stigma; and the place where nectar is secreted; the parts and functions are so organised and correlated as to induce and compel insects, generally bees, in visiting the flowers for nectar, to carry away with them pollen from one flower and bear it to another.

One, perhaps the most striking, of the generalisations in question was as follows:—

"The degree to which the cohesion of the stamens is carried, so remarkable a feature in this tribe, seems to depend on the necessity for access to nectar. In those

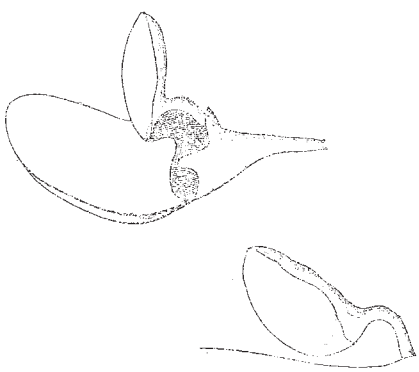

FIG. 1.—Coronilla varia.

flowers in which the stamens are monadelphous, viz. Ulex, Sarathaumus, Genista, Cytisus, Ononis, Lupin, there is no symptom of nectar within the staminal tube, no space for it, and no access to the interior. In some, at any rate, of these, viz. Ulex, Ononis, and Lupin, the bees certainly resort to other parts of the flower. On the other hand, where the tenth stamen is entirely free or where it is separated from the others at the base, so as to give an insect access to the interior of the staminal tube, there is nectar within this cavity."

To this generalisation the two species of *Coronilla* which I had examined, viz. *C. varia* and *C. glauca*, seemed to form an exception. In them the tenth stamen was always separate; but there was no aperture at the base of the staminal tube, no nectar within the staminal tube, and no space for it, the base of the staminal tube fitting as closely round the pistil as it does in those papilionaceous flowers in which the tenth stamen is not separated from the rest.

I have since had an opportunity of examining several species of *Coronilla*, and of watching large plants of *C. varia* (Fig. 1) and *C. emerus* (Fig. 2) in full flower. In all these flowers there is a peculiar structure of the petals. The claw of the vexillum is thin, sometimes prolonged and straight as in *C. emerus;* sometimes shorter and curved as in *C. varia*. The claws of the other petals cohere so as to form a channel, in which the staminal tube lies. But in all cases there is, immediately above the calyx, a large open space between the claw of the vexillum and the claws of the other petals so as to have free access from the outside to the inside or the inside to the outside of the flower.

One hot day last August I watched a bee rifling the flowers of *C. varia* in the regular way. He settled as usual on the lower flowers of the crowded umbel first, resting on the wings and keel, and went rapidly round and up the umbel. The plant was a large one, and he must have been there more than half an hour. He did not seem to be taking pollen. What could he be doing? for there was no semblance of nectar either inside the base of the petals or calyx or inside the staminal tube. On examining the flower carefully with a glass the *outside* of the calyx, which is thick and fleshy, appeared to be covered with shining glands or vessels, sometimes I think moist, but always yielding copious liquid on very slight pressure. Could this be what the bee was seeking? On a subsequent day I again watched a similar bee rifling the flowers, and at last distinctly saw his proboscis, which had entered as usual by the front of the flower, protruded outwards through the gap between the claws of the petals and sweep the outside of the calyx. Here then was an answer to my difficulty. The nectar for which the bee sought the flower, and in getting which he benefited the plant by carrying pollen from flower to flower, was not in any of the usual places inside the flower, but outside the calyx, while there was a very peculiar construction of the petals giving access to it. Instead of proving an anomalous exception to the generalisations I have quoted above, it turns out to be another curious illustration of the various ways in which the same

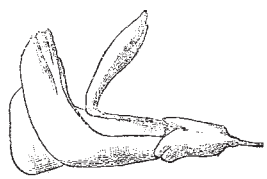

FIG. 2.—Coronilla emerus.

function of secreting nectar and of attracting the bee to it in the manner requisite for fertilising the flower is effected by different organs. That the outside of the calyx should secrete nectar and that there should be a peculiar window, out of which the bee, having entered by the regular door, and having in so doing dusted himself with pollen, should be able to get at the nectar, is surely a remarkable specialisation, and also a remarkable confirmation of the result of generalisations I had previously made.

Since then I have examined some other species or varieties of *Coronilla*, viz. *Coronilla emerus*, a very pretty free flowering garden shrub or creeper, a variety of this named *Coronilla emerus lutescens*, *C. montana*, and *C. minima*.

In *Coronilla emerus* the claws of the petals are much prolonged, so as to make the whole flower much longer than in the other species (see Fig. 2). The structure of the staminal tube is like that of Pisum, Lathyrus, Robinia, &c., in having a large cavity at the base filled with water, and large apertures on each side of the base of the tenth stamen, by which the bee's proboscis can reach the nectar. The long tube or channel formed by the claws of the petals is such as to lead the bee's proboscis directly to these apertures; and I have this spring distinctly seen a humble-bee getting the nectar in this way. The aperture between the claws enabled me to see the bee's proboscis going right down to the base of the staminal tube. On the other hand there is no appearance whatever of nectar or of glands containing nectar outside the calyx.

In *C. emerus lutescens* the structure is the same, except that there is a curious little excrescence on the inside of the claw of the vexillum just above the calyx. Does it

guide the bee's proboscis to the apertures in the staminal tube, which it is to be remembered are on each side of the central tenth stamen? Mr. F. Darwin has suggested a function of this kind for a somewhat similar structure on the free tenth stamen of Phaseolus.

C. montana is a small plant, very like *C. glauca* in structure. The flower forms compact umbels; the claws of the petals are short, with a wide opening above the calyx; the tenth stamen is free, but the staminal tube is close-fitting, and there is no nectar inside the flower. *Per contra*, there are distinct glands or bubbles of liquid on the outside of the calyx, which is much infested by aphis.

C. minima is similar in structure; and both these species or varieties are similar to *C. glauca*.

We have then in this genus a number of species or varieties, all of which have their tenth stamen free, but which differ widely in other respects.

1. In *C. emerus* and *C. emerus lutescens* the nectar is in the base of the staminal tube, and is accessible by the separation of the tenth stamen in the usual manner.

2. In *C. varia*, *C. montana*, *C. glauca*, and *C. minima* the staminal tube is barren of nectar, but the nectar is secreted outside the calyx, and the access to it is provided for by a special gap between the petals.

In both cases, however, the flower is so constructed that the bee in getting the nectar which he wants dusts himself with and carries from flower to flower the pollen.

Some questions remain. The separation of the tenth stamen and the gap between the petals and the separate stamen both exist in all the species; where one is of use the other is useless. Why do they co-exist? Did one exist before the other? and is one of them now useless and rudimentary? If so which was the earlier and which the later in development?

A further observation arises. These *Coronillas* are foreign plants, and in many gardens and greenhouses have only been introduced recently. In my own garden in Surrey I have introduced *C. varia* and *C. emerus* from London within these last four years, and I am not aware of any other plants in the neighbourhood. But the bees seem quite to understand how to get the nectar from both. In *C. emerus* this is not surprising, for there are many other common flowers—Robinia, Pisum, Vicia, Lathyrus, &c.—similarly constructed. But I know of no flower common in England which is like *C. varia* in having the nectar outside the calyx, with the peculiar access to it through a gap in the petals. And yet the Surrey bee found his way to it at once. Does not this look as if the bee had sufficient intelligence to adapt his doings to a perfectly new and unknown structure?

T. H. FARRER

LENZ'S DOCTRINE OF OCEAN CIRCULATION

A VERY elaborate memoir was presented to the Royal Society at its last meeting, by Mr. Prestwich, containing a digest of all the observations made upon deep-sea temperatures previously to the *Lightning* cruise of 1868, which was the starting-point of all those recent researches that have excited so strong and general an interest. Of these observations, some of the most important were quite unknown to the scientific men of the present day, until brought to light by Mr. Prestwich's patient research; and I would take the earliest opportunity of particularly calling attention to those of Emil. Lenz, an eminent German physicist, formerly settled in St. Petersburg,* who accompanied Kotzebue in his second Circumnavigation Voyage in 1823–26. Of this voyage, the obtaining of deep-sea temperatures was one of the special objects; and, with a view to accuracy of observation, experiments were previously instituted by Parrot upon the influence of pressure on self-registering thermometers, of the same kind as those made by Mr. Casella under the late Prof. W. A. Miller and myself in 1869. And the St. Petersburg professors satisfied themselves by their experiments (as we did by ours nearly fifty years later), that any observations taken by sending down ordinary thermometers to great depths must be seriously vitiated by the pressure of the superincumbent water.

Instead of attempting, however, to improve his thermometers by the protecting outer bulb* which made our instruments thoroughly trustworthy, Lenz devised a method of obtaining deep-sea temperatures, which must have been very difficult to work, and which required a good deal of mathematical computation to bring out its results; yet this in his able hands gave temperatures which prove to be in close accordance with the thermometric observations of the *Challenger*. He also made throughout the voyage a careful series of observations on the temperature of the ocean at the surface and at moderate depths below it, which proved to be of the greatest value in the establishment of his general doctrine. And he further made an important series of observations on the salinity of ocean-water as indicated by its specific gravity. The increase of the density of sea-water with the reduction of its temperature down to the freezing-point, was known to Lenz through the experiments of Dr. Marcet in this country, and of Erman in St. Petersburg; and he was consequently free from the influence of the "dominant idea" that the deep water of the ocean, like that of the Swiss lakes, would have the uniform temperature (39½° F.) of *fresh* water at its greatest density; which obviously influenced the conclusions subsequently drawn from their own observations by D'Urville and Sir James Ross, and led to the general adoption of those conclusions.

The whole series of these observations, with the mathematical computations required for the determination of the real bottom-temperatures, are contained in a most elaborate memoir, entitled "Physikalische Beobachtungen, angestellt auf einer Reise um die Welt, unter dem Commando des Capitains von Kotzebue, in den Jahren 1823-26," presented to the St. Petersburg Academy in 1829, and published in vol. i. of its "Transactions" (1831). No one can examine this memoir without being impressed with the remarkable ability it displays; a peculiarly competent judge, Prof. Debus, whose attention I have directed to it, assures me that it is a model of admirable physico-mathematical investigation.

It was not until 1845, however, that Lenz gave forth the general conclusions to which he was led by his own observations and those of others (so far as known to him) in his admirable "Bemerkungen über die Temperatur des Weltmeeres in verschiedenen Tiefen," published in the "Bulletin" of the St. Petersburg Academy for 1847. He there shows that his own conclusions as to the low temperatures obtained at great depths are not invalidated by the observations of others, indicative of higher temperatures taken with ordinary thermometers; but may still be taken as indicating the presence of glacial water on the bottom of each of the great oceans, even under the equator. And from a discussion of the numerous temperature-observations taken at the surface and at small depths beneath it, Lenz deduces the important conclusion *that there is at and under the equator a belt of water cooler than the water to the north and south of it.* Of this striking phenomenon, he says, the explanation flows directly from the form of the isothermal curve which represents it; and this explanation I shall presently reproduce in his own terms, which will be found singularly accordant with those used by myself in the notice I

* The list of Lenz's papers occupies four columns of the Royal Society's Catalogue. A large proportion of them consist of original researches, both experimental and mathematical, in electricity and magnetism. And I am assured by Sir Charles Wheatstone that these are of the highest merit, and were greatly esteemed by Gauss amd Jacobi, the two great masters in this department of investigation.

* It is right to reeall the fact that this "protection" was first devised by Admiral Fitzroy, and was practically worked out by Messrs. Negretti and Zambra, as far back as 1857.